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Abstract

Provision of forage for wild and domestic ungulates, and the associated impacts of their herbivory, are contentious issues for wildland management in western North America. We quantified the composition, above-ground net production (ANP), and utilization of herbaceous and shrub vegetation in five non-forest and seven forest cover types across the core spring-summer-fall range of the Yakima elk herd in the eastern Washington Cascade Range. We randomly sampled each cover type along three elevational transects during a two-year period. Riparian/meadow was the most productive cover type (2,752 kg ha⁻¹ ANP). High-productivity forest at low to high elevations produced 900-1200 kg ha⁻¹ ANP. High-elevation forest and grassland, shrubland, and shrub-steppe produced 600-700 kg ha⁻¹ ANP. The low-productivity forest cover types and parkland produced 100-400 kg ha⁻¹ ANP. Utilization of forbs, grasses, and shrubs combined averaged 47% of ANP across all cover types, ranging from 26% in high-elevation forest to 63% in shrub-steppe. Grasses and forbs were equally utilized at about 57% of ANP, whereas shrubs were utilized at only 4% of ANP. Twenty-two of 55 shrub species accounted for the majority of shrub productivity and showed little to no long-term browsing; but, several shrub species were moderately to severely hedged. Moderate to high levels of ungulate utilization indicate potentially strong impacts of ungulate herbivory on pattern and process in eastern Cascades forests. Dry forest restoration management to reduce fuel loads and restore resiliency to disturbance likely will increase forage for ungulates, especially in closed-canopy true fir and Douglas-fir stands.

Keywords: ungulates, forage, grazing, exotic species, Washington

Introduction

The compatible provision of forage for wild and domestic ungulates, and the associated impacts of their herbivory, have long been important and

contentious issues for wildland management in western North America (Wisdom and Thomas 1996, Belsky and Blumenthal 1997, Vavra 2005) and northern Europe (Kuiters et al. 1996, Gordon et al. 2004). In the Pacific Northwest, those issues also have been critical for population and habitat management of the Yakima elk herd (Mitchell and Lauckhart 1948, Gossett 1964), which is one of the largest elk herds in the state of Washington (WDFW 2002). Populations of native elk were largely decimated in eastern Washington during the latter half of the 19th century from hunting by Native Americans and a burgeoning Euroamerican

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population (McCorquodale 1985, Dixon and Lyman 1996). Elk rapidly became reestablished in the Yakima area from an initial reintroduction of 13 Yellowstone elk during 1913, and by the 1930's the estimated population of 3,000 elk was considered to be significantly contributing, along with heavy and extensive livestock grazing, to near total utilization of forage across the upper Yakima River basin (WDFW 2002).

Grazing of domestic livestock (cattle, sheep, and horses) had been extensive and heavy since the mid-1800s in the Yakima area, which was among the first and most important centers of livestock production in Washington (Wissmar et al. 1994, OWNF 2007). When grazing management was initiated in the new Forest Reserves around 1905, about 260,000 sheep were recorded grazing in the upper Yakima basin, which supported 55% of the sheep and 83% of the cattle and horse grazing in the Yakima valley (Wissmar et al. 1994). Concerns were raised over the condition of the summer ranges as early as 1938, with Forest Service managers blaming poor range conditions on high numbers of elk and sportsmen demanding that all livestock be removed (Mitchell and Lauckhart 1948).

Livestock grazing has been drastically reduced through the twentieth century, but livestock and elk grazing in forested ranges continues to be an issue of forest ecosystem integrity (e.g. overgrazing, exotic species) and a source of conflict among ranchers, farmers adjacent to elk winter range, wildlife managers, and elk enthusiasts (e.g., hunters) (WDFW 2002). Regulated livestock grazing continues to be an important economic use of National Forest lands in the Yakima River drainage (OWNF 2007), and public demand to maintain high elk populations to maximize hunting opportunity or other social values (e.g., viewing) remains high (Vavra et al. 2007, WDFW 2010). However, livestock and elk both are supported by a spring and summer forage base that has declined since the early 1900s with meadow shrinkage (R. Everett, U.S. Forest Service, Wenatchee, WA, unpublished data; see Haugo and Halpern 2007 for general trends in the Cascade Range), development of dense forests due to fire suppression (Everett

et al. 2000, Wright and Agee 2004, Hessburg et al. 2005), regrowth of old burns and pre-1990 clearcuts, and little forest clearcut harvesting as a result of regulatory changes during the last 20 years (Miller and Halpern 1998, Lehmkuhl et al. 2001). There are concerns that sustaining livestock and elk on a shrinking habitat base may have increased or sustained historical degradation of sensitive meadow and riparian habitats (OWNF 2007). The potential effects on elk habitat of dry forest thinning and prescribed burning for new fuels management programs designed to reduce catastrophic fires and restore forest health also are at issue (OWNF 2002).

Knowledge of forage composition, productivity, and utilization (i.e., herbivory) is essential not only for informing wildland management (Hobbs 1996, Lyon and Christensen 2002, Wisdom et al. 2006), but also for understanding animal resource selection (Boyce and McDonald 1999), fitness (Cook et al. 2004), population ecology (Raedeke et al. 2002), and management (Lyon and Christensen 2002). Composition is relatively easy to measure in broad vegetation classes via remote sensing or more finely by field measurement; but, measuring forage productivity remotely or in the field is complicated and difficult because of inherent variability of vegetation, and herbivory can remove forage or stimulate compensatory growth before measurement (e.g., McNaughton et al. 1996). Wildlife resource selection analysis has conventionally used infrared remote-sensing "greenness" indices (Todd et al. 1998, Paruelo and Lauenroth 1998) or field-based standing biomass estimates (e.g., Merrill 1994, Beck and Peek 2004, Anderson et al. 2005) as proxies for habitat productivity. The critical assumption for using either proxy is that consumption by wild and domestic herbivores is inconsequential (Singh et al. 1975); yet, it is well documented that wild herbivore consumption can be substantial (Frank and McNaughton 1993, Frank et al. 1998, Frank et al. 2002) and consumption by domestic livestock is easily estimated from known stocking rates. The failure to measure and adjust for consumption underestimates productivity and its variation among vegetation types (Sala et al. 1988, Biondini and Manske 1996, McNaughton et al. 1996) and

introduces bias from uncorrected forage productivity estimates in resource selection analysis.

Our goal was to develop baseline data that quantifies the composition and production dynamics of herbaceous and woody forage resources within the spring-summer-fall range of the Yakima elk herd. Our objectives were to quantify forage composition (especially exotic and elk-forage species), diversity, and above-ground production and utilization; and, to assess the potential bias in using standing biomass as a proxy for forage productivity or abundance.

Study Area

The Yakima elk herd uses a broad and well-defined area of the high Cascades as summer range, and winters primarily along the lower east slopes of the Cascade Range. The 4,300 km² herd range is bounded by Interstate 90, the Yakima River, the northern boundary of the Yakama Reservation, and the crest of the Cascade Range in south-central Washington. Forested summer and spring-fall transition ranges are mainly on the Naches and Cle Elum Ranger Districts of the Okanogan-Wenatchee National Forest (OWNF). Our study area comprised a 2,500 km² core area of the spring-summer-fall range on the Naches Ranger District.

Low- and mid-montane forests are dominated by open-grown ponderosa pine (*Pinus ponderosa*) at the lowest elevations (600 m), with increasing dominance of Douglas-fir (*Pseudotsuga menziesii* [PSME]) and grand fir (*Abies grandis* [ABGR]) as elevation increases up to about 1200 m. Upper montane forest dominated by subalpine fir (*A. lasiocarpa* [ABLA]), with silver fir (*A. amabilis*) and mountain hemlock (*Tsuga mertensiana*), occur up to the crest of the Cascade Range at about 1500 m elevation. Parklands, a mosaic of subalpine fir and dry meadows, and steep rocky areas are common at high elevations (1700 m). Winter range is mostly on Washington State lands in shrub-steppe or dry grassland vegetation at about 300 m elevation. Shrub-steppe and dry grasslands are dominated by native bunchgrasses, exotic annual grasses (*Bromus tectorum*), and big sagebrush (*Artemisia tridentata tridentata*). The

herd range is typical of many elk ranges in the interior Pacific Northwest.

In recent years, the Yakima elk herd has ranged from an uncertain high of 15,036 elk in 1999 to 8,589 in 2010 (WDFW 2010). The estimated elk population size during the study (2005-2006) was 8,851-9,589 elk, co-occurring with roughly 5,300 mule deer (*Odocoileus hemionus*) (WDFW 2010). The ecological density of elk on the summer range was approximately 3.3 elk km⁻² based on an average population of 9,220 elk during the study period and an estimated 2,800 km² of habitat that includes 95% of elk radiotelemetry locations recorded in a separate study (P. Singleton, US Forest Service, Wenatchee, WA, unpublished data). The similarly approximated winter range density is 4.6 elk km⁻². Assuming similar summer and winter ranges for the mule deer herd, the summer-range density of deer is roughly 1.9 deer km⁻² and the winter-range density is 2.6 deer km⁻². Thus, the total wild ungulate density is about 5.2 animals km⁻² on the summer range and 7.2 animals km⁻² on the winter range.

During the study period a combined 2,667 cow/calf (567 [21%]) and ewe/lamb (2,100 [79%]) pairs were grazed annually on Forest Service lands in five separate grazing allotments over an average 78-day (sheep) to 117-day (cattle) period from about June 1 to September 30. The stocking rate totaled 7,487 "head-months": 30% from cow/calf pairs and 70% from ewe/lamb pairs. A head-month is the Forest Service equivalent of an animal-unit-month (AUM), which is defined as the amount of forage required by a standardized animal unit for one month. The standard animal unit is a 455 kg (1,000 lb.) mature cow with a consumption rate of 9.1 kg (20 lb.) forage day⁻¹, or 372 kg (820 lb.) month⁻¹ (Holechek et al. 1995). Stocking rates (head-months) for other classes of livestock (e.g., cow/calf or ewe/lamb pairs) and wild ungulates are estimated as a proportion of that standard based on unit (individual animal) body weights, forage consumption rates, and local forage productivity (i.e., quantity and quality). In the study area, forage requirements used to manage grazing are: cow/calf pair, 455 kg (1,000 lb.) forage month⁻¹; ewe/lamb pair, 90

kg (200 lb.) forage month⁻¹; elk, 225 kg (500 lb.) forage month⁻¹; and deer, 100 kg (222 lb.) forage month⁻¹ (OWNF 2007). The total annual stocking rate (livestock plus wild ungulates) of the study area is estimated at 78,103 head-months, based on 55,320 elk head-months (71%), 15,296 mule deer head-months (19%), and 7,487 head-months of domestic livestock (10%).

Climate in the study area is continental with cold snowy winters and warm dry summers. Mean cumulative precipitation for the water years (October-September) from 1988 through 2005 was 162 cm (NRCS 2008). Mean minimum temperature for that period was -5.6 °C during February, and mean maximum temperature was 22 °C during August. Climate during the study year 2006 was similar to the 1988-2005 17-year average in terms of cumulative precipitation (161 cm) and mean daily temperatures. The study year 2005 was dryer and warmer than 2006 and the 17-year average. Precipitation during the 2005 water year was 70% (114 cm) of the long-term average and about half the 2006 precipitation. Mean daily temperature during winter through April 2005 consistently was ~3 °C warmer than during 2006. Summer temperatures were similar during 2005 and 2006.

Methods

Field Sampling

Cover Type Definition—We initially mapped 19 non-forest and forest cover types for field sampling from existing GIS (Geographic Information System) map data (Table 1). We based our initial cover type classes on a preliminary analysis of elk use from telemetry relocations and availability. Mapped cover types were designed to typify elk habitat in a classification that was feasible for replicated field sampling over the large study landscape. The Yakima elk herd ranges over numerous jurisdictions, so we combined maps of existing vegetation from an existing elk habitat assessment (P. Singleton, US Forest Service, Wenatchee WA, unpublished report), the Naches Ranger District, the Washington Dept. of Natural Resources, the Yakama Nation, the Washington Department of Fish and Wildlife, and private landowners.

We defined the initial 12 forest cover types based on three dominant forest cover types, open ($\leq 40\%$) or closed ($>40\%$) forest canopy, and north vs. south aspects (Table 1). Forest cover types were: 1) lower montane ponderosa pine, Douglas-fir, and dry grand fir forests (designated as PSME cover types), 2) mid-montane mesic grand fir and western hemlock forests (designated as ABGR cover types), and 3) upper montane silver fir, mountain hemlock, and subalpine fir forests (designated as ABLA cover types). Our canopy-cover threshold is somewhat arbitrary and may encompass a wide range of understory production, if production is a linear function of canopy cover (McConnel and Smith 1970); but, Young et al. (1967) found a strong 36-50% canopy cover threshold defining low vs. high herbaceous and shrub production in mixed-conifer forests of the similar nearby Blue Mountains. We mapped seven non-forest cover types: riparian areas, mesic mid-elevation meadows, dry steppe grassland, alpine parkland, mid- and high-elevation shrublands, rock fields in shrublands, and low-elevation shrub-steppe.

We measured a stratified random sample of each initial cover type along each of three elevational corridors (strata) to yield at least three replicate sample sites per initial cover type. We chose sample locations for each cover type randomly from the pool of mapped stands located within 1.5 km of three primary highways (i.e., the corridors) that transect the study area from east to west. We also sampled species composition at a selection of random sites away from corridors to boost sample size of riparian, meadow, and grassland cover types, especially in high-elevation wilderness areas and portions of the low-elevation winter range. Many sample locations outside wilderness areas were near roads, which might be expected to depress elk use (Rowland et al. 2000), hence underestimate utilization; however, the managed portion of the study area is highly roaded and separate analysis of extensive radio-telemetry data showed no effect of distance from road on elk site selection (P. Singleton, US Forest Service, unpublished data). Our samples were on lands managed by the US Forest Service (nearly all the summer range) and the WDFW (mostly winter range).

TABLE 1. Original cover types sampled for composition and productivity in the core 2,500 km² spring-summer-fall range of the Yakima elk herd in the Naches River basin of the eastern Washington Cascade Range for the 2005 and 2006 period, correlated with the combined cover types for which composition, productivity, and utilization are reported, and percentage area of each combined type in the study area.

Original cover types ¹	Combined cover types ²	Percentage area
<u>Forested</u>		
PSME, open canopy, south aspect	PSME low productivity	5
PSME, closed canopy, north aspect	"	
PSME, closed canopy, south aspect	"	
PSME, open canopy, north aspect	PSME high productivity	3
ABGR, closed canopy, north aspect	ABGR low productivity	7
ABGR, closed canopy, south aspect	"	
ABGR, open canopy, north aspect	ABGR high productivity	33
ABGR, open canopy, south aspect	"	
ABLA, closed canopy, north aspect	ABLA low productivity	3
ABLA, closed canopy, south aspect	"	
ABLA, open canopy, north aspect	ABLA moderate productivity	15
ABLA, open canopy, south aspect	ABLA high productivity	12
<u>Non-forest</u>		
Riparian	Riparian/meadow	3
Mid-elevation meadow	"	
Dry grassland	Grassland	1
Alpine parkland	Parkland	2
Shrubland	Shrubland	18
Rock	"	
Shrub-steppe	Shrub-steppe	na ³

¹ PSME—Douglas-fir, ABGR—grand fir, ABLA—subalpine fir dominated. Open canopy is ≤40% closure, closed canopy is >40%.

² Low, moderate, or high refer to relative annual net productivity as determined by field sampling.

³ Percentage area not applicable. Shrub-steppe is primarily winter range and was sampled outside the core spring-summer-fall range.

After completing field work and a preliminary floristic analysis we used hierarchical cluster analysis of floristics and results from preliminary analysis of understory productivity to group the initial 19 cover types into seven forest and five non-forest cover types, characterized by dominance of PSME, ABGR, or ABLA and low (< 400 kg ha⁻¹), moderate (400-900 kg ha⁻¹), or high (>900 kg ha⁻¹) understory primary productivity (Table 1). This allowed us to create a smaller analysis set and pool similar samples to increase sample size for each cover type (Table 1).

Understory Composition and Productivity—At each sample site, we defined a 30 x 35 m “macro-plot” that contained three parallel 30-m transects.

We sampled plots at the beginning of the growing season in spring (May, June) and at the end of the growing season (August, September, October) during 2005 and 2006. The timing of sampling visits varied by cover type to coincide with snow melt, green-up, and vegetation dormancy. For example, we sampled low-elevation sites in hot-dry shrub-steppe during August after dormancy, but sampled high-elevation meadows at the end of the summer growing season during October. We estimated percent cover of each plant species < 1m tall as the average vertical projection of the plant crown, or area, in nine 0.5-m² quadrats (3 per transect). Shrubs and trees >1 m tall were measured with the shrub protocol (below). We measured annual herbaceous above-ground net

production (ANP) and utilization from three caged-plot pairs per macroplot during 2005 and 2006. We clipped samples within 1 cm of the ground surface from 0.5-m² plots located inside and outside movable grazing cages (1.5 m x 1.5 m) (Frank et al. 2002) placed on the site the previous autumn. We pooled clipped biomass into graminoid and forb categories. We bagged and dried samples at 60 °C for 24-48 hours prior to obtaining dry matter weights.

Shrub Productivity—We estimated annual shrub production and utilization at the end of the growing season in late summer or early fall, depending on phenology at different elevations. We used the non-destructive weight-unit (also called reference-unit) method (Bonham 1989, BLM 1996) for sampling shrub production on the permanent macroplots. We measured only current-year growth that was considered forage and within reach of elk (≤ 2.3 m above ground on the upslope side). We defined forage as new twigs and leaves, but not old wood. We considered conifers ≤ 2.3 m tall as shrubs if designated as elk or deer browse.

We measured shrubs in four 3 x 13.5 m permanent rectangular plots (40.4 m²) at each corner of the macroplot. We recorded the number of weight-units for each species, the percent of current year weight-units that had been browsed, and the average percent of a weight-unit removed by browsing. We classified shrub hedging and age (seedling, young, mature, decadent), and estimated a growth adjustment factor to adjust for sampling before peak production at a site (BLM 1996). The growth adjustment factor measured the cumulative percent of the potential annual growth attained at the time of measurement (scale 1-10 with 1 = 10% and 10 = 100% of potential annual growth for that year). We then clipped a reference set of weight-units for that macroplot from 2 destructive-sampling plots adjacent to the macroplot. We harvested the first six weight-units encountered on different plants in each of two plots for a total sample of up to 12 weight-units for each species. We collected only current-year forage from a weight unit. We bagged and dried samples at 60 °C for 24-48 hours prior to obtaining dry weights.

Analysis

Floristic Analysis—We summarized the mean composition and species richness of cover types by dominant and forage species across locations and two sampling years. We developed a list of 20 primary herbaceous and shrub forage species used by deer and elk based on Cook (2002), local expertise of wildlife biologists, and a preliminary analysis of plant parts in fecal samples (A. Lyons, Okanogan-Wenatchee National Forest, Wenatchee, WA, unpublished data). Elk diets are notoriously variable among locations, seasons and years (Cook 2002), so our short list is not exhaustive. We characterized the floristic similarity among vegetation cover types, excluding rare species ($< 5\%$ frequency), by ordination with non-metric multidimensional scaling (NMS). We used Indicator Species Analysis (ISA) to identify indicator, or characteristic, species found mostly in a single cover type and present in the majority of the sites belonging to that cover type (Dufrene and Legendre 1997). Such indicator species might be of particular interest to managers attempting to manage particular cover types or species. ISA combined information on both species relative abundance (cover) and constancy to estimate indicator value for each species in each group. The maximum indicator value of a species within our 12 cover types was tested for statistical significance ($P \leq 0.05$) against the random expectation calculated by 1,000 Monte Carlo permutations. All floristic analyses were done in Program PC-ORD version 5.0 (MjM Software, Gleneden Beach, OR, USA).

Productivity—We estimated graminoid and forb ANP and utilization at each sample location from the paired caged-plot data using Method 1 of McNaughton et al. (1996):

$$\begin{aligned} \text{ANP} &= (\text{utilization}_{11} + \text{utilization}_{12}) + \text{outbiomass}_{12} \\ \text{Utilization} &= \text{utilization}_{11} + \text{utilization}_{12} \end{aligned}$$

where utilization₁ was the mean difference between inside cage biomass and outside cage biomass for the three paired caged-plots, and outbiomass₁₂ was the mean biomass outside cages at the second sample period. We adjusted negative utilization values (i.e., when outside-cage grazed biomass was greater than ungrazed biomass inside the cage due

to sampling variation) by setting utilization to zero. Mean and standard error of ANP and utilization were estimated separately for 2005 and 2006. The proportion of ANP consumed was calculated as the ratio of mean utilization and mean ANP for each year. Annual production and utilization for the study period was estimated as the mean of both years, and percentage utilization as the ratio of mean utilization and production.

We estimated shrub production and utilization for individual shrub species at each sample location as the mean value of the four subplots. Production and utilization for a cover type were the sum of species values. Production was first calculated by multiplying the number of weight units by the mean dry weight of individual weight units and the growth adjustment factor. We then added the estimated utilization, which was calculated as the product of the proportion of stems browsed and the proportion of individual stems removed. This might have resulted in end-of-growing season estimates that underestimated utilization for some species browsed during the winter; but, we felt that over-winter utilization estimates were problematic because we could not account for variable winter weather and its effects on ungulate herbivore distribution and browsing pressure during two years of sampling. We estimated long-term browsing pressure on species as the proportion of plants of a species in different form classes (BLM 1996) to estimate long-term browsing impacts. We made only one estimate of total shrub production for the study (i.e., not annual estimates) because some cover types were sampled in only one year for logistical reasons.

Results

Composition

The riparian/meadow cover type had the greatest species-richness. The total number of species recorded (324) was 2-10 times greater than in other cover types (Table 2). However, mean richness per sample plot (23.1) was similar to other productive cover types indicating infrequent occurrences of many uncommon species and high species heterogeneity among riparian/meadow locations. Exotic species accounted for an aver-

age 13% of plot richness and 18.5% of the total cover in riparian/meadow types. Grasses and grass-like plants (i.e., graminoids) dominated the riparian/meadow cover type (Table 3). The exotic grass *Poa pratensis* had the highest cover among all species and was highly characteristic (i.e., an indicator species) of the riparian/meadow cover type. Several native *Carex* spp. and *Agrostis* spp. were the most abundant graminoid species. *Calamagrostis canadensis* was an indicator native grass species. Forb cover was about half that of graminoids. *Trifolium repens* and *Plantago lanceolata*, two exotic forbs, were indicator species of the riparian/meadow cover type. *Carex*, *Poa*, *Trifolium*, *Calamagrostis*, and *Bromus* species were the most abundant forage genera (Table 3).

The low- and mid-montane PSME and ABGR cover types were relatively similar in composition compared to other types (Figure 1). Exotic species were infrequent, averaging ≤ 1.1 per plot and represented $< 2\%$ of total understory cover (Table 2). Low-productivity cover types averaged 16-20 species, mostly herb and graminoid species, and high-productivity cover types had 23-26 species. The PSME-low understory was relatively depauperate, with about 6% cover each of forbs and graminoids, compared to the PSME-high cover type with nearly 2x more forb cover, 50% more graminoid cover, more Douglas-fir regeneration cover, and 50% more shrub cover. In both low- and high-productivity PSME cover types, the forage species *Carex geyeri* and *Calamagrostis rubescens* were the dominant graminoids (Table 3). The PSME-low cover type had few (2) indicator species, but the PSME-high cover type had 14 indicator species, most importantly the forage species *C. geyeri*, *Purshia tridentata*, *Ribes cereum*, and *Symphoricarpos oreophilus* (Table 3).

The ABGR cover types differed principally from the PSME cover types in having uniformly lower forb cover compared to PSME cover types, but about 5x higher shrub cover regardless of productivity class (Table 2). ABGR cover types were similar to PSME cover types in the contribution of shrubs to the forage base, except for high cover of *Mahonia* species in the ABGR-low cover type. Graminoid cover in ABGR-low cover type was

TABLE 2. General environmental and average understory vegetation characteristics of 12 forest and non-forest cover types of the Naches River basin in the southeastern Washington Cascade Range, 2005-2006. Percentage cover and richness are mean values for 0.5 m² plots.

Habitat ¹	No. sites	No. plots ²	Elevation (m)	Total spp.	total cover (%)	Exotic					Native richness (n spp.)	Total richness (n spp.)	
						Forb cover (%)	Graminoid cover (%)	Shrub cover (%)	Tree cover (%)	Exotic richness (n spp.)			
Forested													
PSME low	9	27	910	120	14	trace	6	6	1	1	0.7	17.9	19.6
PSME high	4	10	1015	93	25	trace	11	9	1	3	1.1	22.3	25.7
ABGR low	8	20	1130	81	12	0	4	1	6	1	0.0	15.7	16.1
ABGR high	8	20	1150	133	20	trace	5	8	4	3	1.1	20.4	23.2
ABLA low	9	21	1290	55	8	0	1	0	4	3	0.0	11.6	11.8
ABLA moderate	5	11	1400	110	24	trace	9	3	9	4	0.8	27.1	29.2
ABLA high	6	12	1480	115	22	1	9	4	4	5	0.8	20.3	22.4
Non-forest													
Riparian/													
meadow	32	43	1210	324	23	4	8	13	1	trace	3.1	16.4	23.1
Grassland	3	9	1300	79							0.8	19.2	21.6
Parkland	10	16	1680	115	16	1	7	8	1	0	0.3	17.4	19.6
Shrubland	10	19	1070	137	21	trace	5	3	9	3	2.2	18.7	21.5
Shrub-steppe	2	4	1170	31	11	1	6	4	1	0	5.5	8.5	15.0

¹ PSME—Douglas-fir, ABGR—grand fir, ABLA—subalpine fir dominated. Low, moderate, and high descriptors refer to classes of combined forb, graminoid, and shrub primary productivity as determined during the study.

² Number of plots is a combination of random sites sampled in one year, plus 2 annual (2005-2006) measurements of permanent plots on three landscape transects.

TABLE 3. Mean percentage cover and total life-form cover of elk forage genera in 12 cover types of the Naches River basin in the southeastern Washington Cascade Range, 2005-2006.

Life-form	Genus	PSME low ¹	PSME high	ABGR low	ABGR high	ABLA low	ABLA mod.	ABLA high	Riparian/meadow	Grass-land	Park-land	Shrub-land	Shrub-steppe	Mean	
Forb	<i>Balsamorhiza</i> (2) ²	trace ²		trace						trace	trace	trace ⁴	trace	trace	
	<i>Eriogonum</i> (7)	trace	trace	trace	trace	2	2	1	trace	trace ⁴	1 ⁴	trace ⁴	trace	trace	
	<i>Lupinus</i> (4)		trace			trace	trace	trace ⁴	trace	trace		trace	trace	1	
	<i>Senecio</i> (3)	1				trace	trace	trace	1 ⁴	trace ⁴	trace	trace	trace	trace	
	<i>Trifolium</i> (4)	1	1	trace	trace	2	2	1	1	trace	2	1	trace	1	
	subtotal														
	Graminoid	<i>Bromus</i> (9)	trace	trace	trace	trace	trace	trace	trace	1	1	trace	1	1 ⁴	trace
		<i>Calamagrostis</i> (3)	2	4	trace	5 ⁴	trace	trace	trace	1 ⁴	1	trace	trace	1	1
		<i>Carex</i> (24)	3	4 ⁴	1	2	2 ⁴	2 ⁴	3	6 ⁴		1	trace	2	2
		<i>Festuca</i> (5)	trace	trace	trace	trace	trace	trace	trace	trace	2 ⁴	0.8	trace	trace	trace
<i>Juncus</i> (7)			trace						trace	trace	trace	trace	trace	trace	
<i>Poa</i> (7)		1 ⁴	trace		trace			trace	2 ⁴	1	trace	2	2 ⁴	1	
<i>Pseudoroegneria</i> (1)		trace						trace	trace			1	3 ⁴	1	
<i>Stipa/Achnatherum</i> (2)		trace	trace	1	8	trace	trace	trace	trace	5	2	1	1	1	
subtotal		6	9	1	8	trace	2	3	2	7	2	4	7	5	
Shrub		<i>Acer</i> (1)								trace					trace
	<i>Amelanchier</i> (1)	trace	trace	trace	trace									trace	
	<i>Ceanothus</i> (1)				trace									trace	
	<i>Chrysothamnus</i> (2)											trace		trace	
	<i>Holodiscus</i> (1)													trace	
	<i>Mahonia</i> (2)													trace	
	<i>Prunus</i> (1)													trace	
	<i>Purshia</i> (1)	trace	trace ⁴											trace	
	<i>Ribes</i> (5)		trace ⁴											trace	
	<i>Rosa</i> (2)		trace	1 ⁴	1	trace	1	1	4 ⁴	trace			trace	1	
	<i>Salix</i> (2)													trace	
	<i>Spiraea</i> (2)		trace	trace	trace	1 ⁴	trace	trace			trace	trace		trace	
	<i>Symphoricarpos</i> (3)	trace	1 ⁴	1	trace	trace	trace	trace	trace	trace	trace	trace	trace	trace	
	subtotal	1	1	4	1	trace	2	4	4	1	trace	trace	trace	1	
	Total	8	1	5	9	trace	6	8	12	7	4	5	7	7	

¹ PSME—Douglas-fir, ABGR—grand fir, ABLA—subalpine fir dominated. Low, moderate, and high descriptors refer to classes of forb, graminoid, and shrub primary productivity as determined during the study.

² Number of species within genera encountered in sample plots.

³ Trace < 1% cover.

⁴ Genera with one or more indicator species in the cover type. See text for species name.

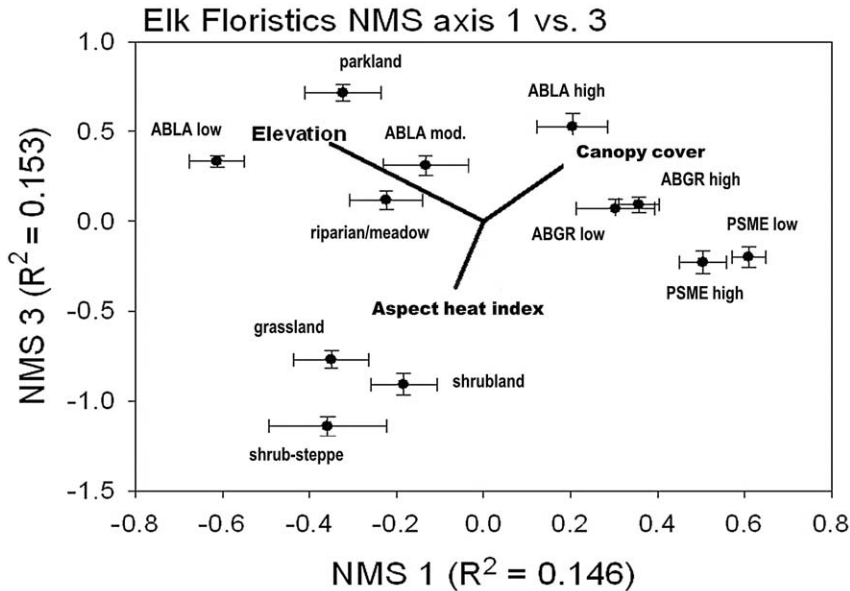


Figure 1. Ordination of cover types and important environmental variables by non-metric multidimensional scaling of floristic composition in the Naches River basin in the southeastern Washington Cascade Range, 2005-2006.

markedly low (1.25%), whereas graminoid cover in ABGR-high cover type (8.09%) was comparable to PSME-high cover type (8.61%), mostly *Carex geyeri* and *Calamagrostis rubescens*. *C. rubescens* also was strong indicator species of the ABGR-high cover type, i.e., cover was consistently high and constant among sample plots.

High-elevation parkland was floristically similar to the ABLA cover types (Figure 1, Table 2). *Carex* and *Festuca* graminoids and the *Lupinus* forb species contributed most to forage species cover.

The low-montane grassland and shrubland cover types and shrub-steppe were very similar floristically (Figure 1). Grassland was moderately rich in total species (79) with few exotic species. *Achnatherum lemmonii* (formerly *Stipa*) and *Festuca idahoensis* dominated graminoid cover and were the primary forage species. Grasslands were floristically unique in having among the highest number (11) of indicator forbs.

Shrub-steppe and montane shrubland were floristically similar primarily in the high cover of the grasses *Pseudoroegneria spicata*, *Poa secunda*, and *Bromus tectorum*; yet, shrub-steppe differed from shrubland in several important ways. Shrub-

steppe was the most species poor (31 spp.) of all cover types and had the second-highest number of exotic species (Table 2). Although shrub-steppe had slightly fewer exotic species than the riparian/meadow cover type, exotic species strongly characterized the shrub-steppe plant community: eight (57%) of the 14 indicator species in shrub-steppe were exotic forbs (5) and graminoids (3) compared to three exotic species (38%) among eight indicator species in the riparian/meadow cover type. Exotic intermediate wheatgrass (*Thinopyrum intermedium*) and native bluebunch wheatgrass (*P. spicatum*) were the dominant grasses in shrub-steppe. Grasses had relatively higher cover than forbs in shrub-steppe compared to shrublands (Table 2), and sagebrush (*Artemisia tridentata*) was the dominant shrub in shrub-steppe.

Productivity

Riparian/meadow was the most productive cover type, with more than 2x greater herbaceous and shrub production than other cover types, producing an average 2,752 kg ha⁻¹ over both years of the study (Figure 2). The high-productivity PSME, ABGR and ABLA forest cover types as a group

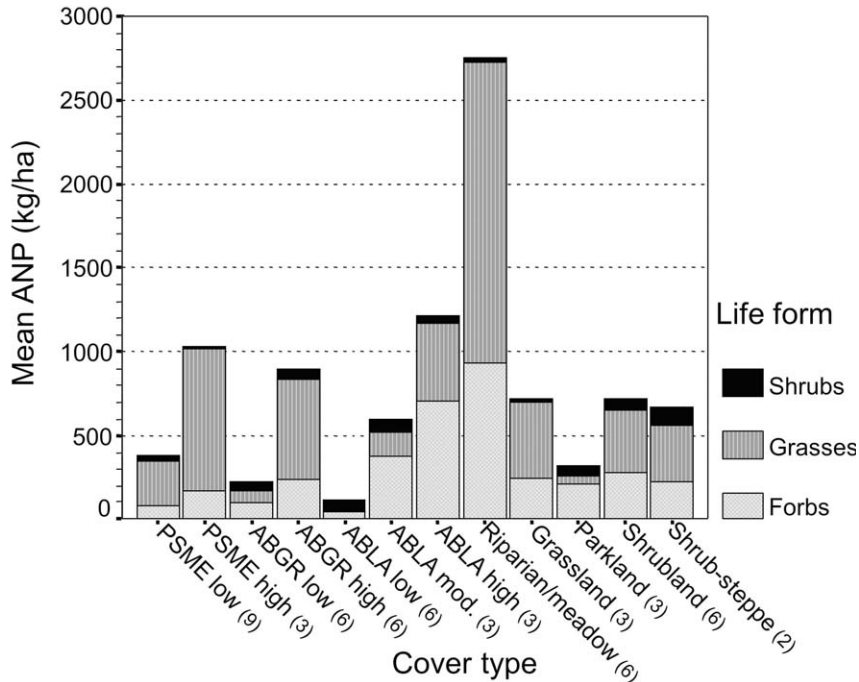


Figure 2. Mean contributions of forbs, graminoids, and shrubs to total above-ground net primary production in cover types in the Naches River basin in the southeastern Washington Cascade Range, 2005-2006. The numbers of sample locations follows cover type names in parentheses.

ranked second in productivity, producing from about 900-1200 kg ha⁻¹ understory biomass. The ABLA-moderate and non-forest grassland, shrubland, and shrub-steppe cover types as a group ranked third in understory productivity, producing 600-700 kg ha⁻¹ herbaceous and forage shrub biomass. The low-productivity PSME, ABGR and ABLA forest cover types and parkland ranked fourth in productivity, producing 100-400 kg ha⁻¹ herbaceous and shrub biomass.

In the riparian/meadow cover type, graminoids constituted 65% (1796 kg ha⁻¹) of the annual production (Figure 2). *Carex*, *Poa*, and *Calamagrostis* genera had the greatest cover among the forage graminoid genera (Table 3). The remainder of production was from forbs (34%, 932 kg ha⁻¹), and a minor contribution from shrubs (1%, 24 kg ha⁻¹). *T. repens* was the most abundant forage forb in terms of cover. *Alnus incana* was the most productive shrub, followed by the *Salix* spp. and *Symphoricarpos albus* (Table 4), both identified forage species.

Among the other non-forest cover types, annual productivity of montane grassland (723 kg ha⁻¹), shrubland (722 kg ha⁻¹), and shrub-steppe (673 kg ha⁻¹) were similar, with grasses accounting for 51% (shrubland, shrub-steppe) to 62% (grassland) of the production (Figure 2). The shrub component of production was greatest in shrub-steppe (16%), followed by shrubland (10%), and grasslands (3%). *Artemisia tridentata* dominated shrub-steppe shrub production, whereas forage species *Chrysothamnus viscidiflorus* and *Eriogonum heracleoides* contributed a small amount of forage (Table 4). In shrublands, *Artemisia arbuscula* and *Arctostaphylos nevadensis*, *Eriogonum* spp., and *Purshia tridentata*, the latter two both forage species, were the main producers. In grassland, *A. arbuscula* dominated shrub production, with *Eriogonum douglasii* producing a small amount of forage. Alpine parkland produced the least among the non-forest cover types (324 kg ha⁻¹). Forbs dominated (67%) parkland production, followed by shrubs (19%) and grasses (15%). *Lupinus*,

TABLE 4. Mean annual production (kg ha⁻¹) of shrub and tree forage ≤2.3 m above ground by cover type in the Naches River basin in the southeastern Washington Cascade Range, 2005-2006.

Species	PSME low ¹	PSME high	ABGR low	ABGR high	ABLA low	ABLA mod.	ABLA high	Riparian/meadow	Grass-land	Park-land	Shrub-land	Shrub-steppe
<i>Abies amabilis</i>					15.6	0.6				4.7		
<i>A. grandis</i>	trace ²		2.2	4.1	1.5	4.5	1.1	trace			0.1	
<i>A. lasiocarpa</i>					0.6		5.1	0.1		3.9		
<i>Acer glabrum douglasii</i> ³	trace		0.3		trace			0.1				
<i>Alnus incana</i>							13.6					
<i>Amelanchier alnifolia</i> ³	1.5	0.5	0.2	trace								
<i>Arctostaphylos nevadensis</i>	0.1		0.1	12.9					18.9	3.2		
<i>Artemisia arbuscula</i>		1.1									13.5	
<i>A. rigida</i>											12.7	
<i>A. tridentata</i>											4.0	102.9
<i>Ceanothus velutinus</i> ³				0.5								
<i>Chimaphila umbellata</i>	1.5		0.2	1.3								
<i>Chrysothamnus viscidiflorus</i> ³												0.6
<i>Cornus sericea sericea</i>								trace				
<i>Ericameria bloomeri</i>	1.0										0.3	
<i>Eriogonum compositum</i> ³											0.9	
<i>E. douglasii</i> ³									3.0		5.7	
<i>E. heracleoides</i> ³											12.9	0.2
<i>E. thymoides</i> ³											2.9	
<i>E. umbellatum</i> ³											0.1	
<i>Holodiscus discolor</i> ³	3.1	0.6		trace								
<i>Juniperus communis</i>										0.4		
<i>Larix occidentalis</i>				trace								
<i>Ledum glandulosum</i>								0.1				
<i>Linnaea borealis longiflora</i>			4.6	5.6	11.5	13.1	0.6					
<i>Mahonia aquifolium</i> ³	3.1	1.3	9.1	0.9		0.6		0.4				
<i>M. nervosa</i> ³	1.2		26.8	6.9	5.4	2.4	1.7					
<i>Menziesia ferruginea</i>					0.2	1.5						
<i>Paxistima myrsinites</i>			1.5	1.7	1.2	13.2				0.5		
<i>Penstemon davidsonii</i>												2.8

Species	PSME low ¹	PSME high	ABGR low	ABGR high	ABLA low	ABLA mod.	ABLA high	Riparian/meadow	Grass-land	Park-land	Shrub-land	Shrub-steppe
<i>Philadelphus lewisii</i>	0.8										3.7	
<i>Phlox diffusa</i>												3.0
<i>P. longifolia</i>												
<i>Picea engelmannii</i>				trace	0.1		5.2					
<i>Pinus albicaulis</i>						0.1		trace		0.1		
<i>P. contorta</i>				8.7								
<i>P. monticola</i>					0.1							
<i>P. ponderosa</i>	trace	5.2		1.0								
<i>Pseudotsuga menziesii</i>	trace	trace	0.1	0.6	0.3	0.5	0.7				0.1	
<i>Purshia tridentata</i> ³	0.5	0.7									9.1	
<i>Ribes lacustre</i> ³				0.2	trace	2.2	0.1	1.7				
<i>R. viscosissimum</i> ³						1.7	31.7					
<i>R. watsonianum</i> ³								0.7			0.1	
<i>Rosa gymnocarpa</i> ³	1.1	0.2	3.0	2.9	0.2	9.6	0.5	1.2				
<i>Rubus leucodermis</i>				trace								
<i>Sambucus cerulea</i>				trace								
<i>Salix</i> spp. ³								6.3				
<i>Salix scouleriana</i> ³				2.8								
<i>Shepherdia canadensis</i>				trace								
<i>Spiraea betulifolia lucida</i> ³	1.8	0.3	1.3	3.3	0.1	3.6						
<i>Symphoricarpos albus</i> ³	16.0	5.8	1.4	0.5		0.2	trace	2.3			0.1	
<i>Tsuga heterophylla</i>			trace									
<i>Vaccinium membranaceum</i>			1.5	1.3	6.3	14.3	1.3			2.5		
<i>V. myrtillos</i>			0.2									
<i>V. scoparium</i>			0.8	3.2	21.5	8.0	1.2			61.0		
Total	31.8	15.8	53.3	58.5	64.5	76.0	49.4	26.6	21.9	76.3	69.0	106.6

¹ PSME—Douglas-fir, ABGR—grand fir, ABLA—subalpine fir dominated. Low, moderate, and high descriptors refer to classes of forb, graminoid, and shrub primary productivity as determined during the study.

² Trace is <0.1 kg/ha

³ Elk key forage species in study area.

Carex, and *Festuca* spp. were the primary forage taxa (Table 3).

Open-canopy, south-facing subalpine fir stands (ABLA-high) were the most productive (1215 kg ha⁻¹) of the forested cover types (Figure 2). Forbs constituted most (58%) of the production, followed by grasses (38%). Among the forage species, *Lupinus* spp. had the highest forb cover, and *Carex* spp. had the highest graminoid forage cover. The most productive forage shrub was *Ribes viscosissimum* (Table 4). Subalpine fir stands with open canopies on north aspects (ABLA-moderate) produced less than half the biomass of ABLA-high stands. *Carex* was the most important forage graminoid in terms of cover, and *Rosa gymnocarpa* and *Ribes* spp. produced the most shrub forage (Table 4). Closed-canopy subalpine fir stands on all aspects (ABLA-low) were the lowest producing cover type (107 kg ha⁻¹) measured, with production mostly (60%) from shrubs followed by forbs (39%). *Mahonia* spp. were the highest producing shrubs, and no single forage forb was identified from cover data (Table 3).

Low- and mid-elevation PSME-high stands with open canopies on north aspects and ABGR-high stands with open canopies on all aspects were nearly as productive as ABLA-high stands, annually producing 1030 kg ha⁻¹ and 899 kg ha⁻¹, respectively (Figure 2). In contrast to forb-rich ABLA stands, graminoids dominated the production of PSME-high (82%) and ABGR-high (67%) stands, mostly the forage genera *Carex* and *Calamagrostis* (Table 3). *Symphoricarpos albus* and *Mahonia* spp. provided the most forage shrub biomass in PSME-high, whereas *Mahonia nervosa*, *Spiraea betulifolia*, *Rosa gymnocarpa*, and *Salix scouleriana* were the most productive shrubs in ABGR-high. *Carex* and *Calamagrostis* graminoid forage also dominated (72%) the relatively low production (384 kg ha⁻¹) of PSME-low stands with closed canopies on all aspects and open canopies on south aspects. *S. albus* was the dominant shrub forage (Table 4). ABGR-low stands with closed canopies on all aspects stands had low productivity (225 kg ha⁻¹), and were notable for a mix of forage groups. *Mahonia nervosa* was the dominant shrub forage at those sites (Table 4).

Utilization

Utilization by all herbivores of combined forb, graminoid, and shrub ANP averaged 47%, ranging from 26% in the ABLA-low cover type to 63% in shrub-steppe (Figure 3). Across all cover types, graminoids and forbs were equally utilized at about 57% utilization, whereas shrubs overall showed only about 4% average utilization. Across all sample locations, utilization was strongly ($R^2 \geq 0.92$) and linearly predicted by ANP ($P < 0.001$), but utilization varied more (i.e. deviated from the mean relationship with ANP) among sample locations with low ANP (PSME-low, ABGR-low, ABLA-low) compared to sites with high ANP (Figure 4). A quadratic relationship between utilization and ANP in forested cover types was not significant ($P = 0.121$). Among forested cover types, utilization at low-productivity ABLA sites and some low-productivity ABGR sites was far less than predicted by ANP, and utilization as a percentage of ANP tended to be lower than in high-productivity forest cover types (Figure 4A). In contrast, utilization at relatively low-productivity sites in the PSME and ABGR series tended to be higher than predicted, but relatively similar to the highest productivity sites.

Twenty-two of the 55 shrub species recorded accounted for the majority of shrub productivity among cover types (Table 4). Many of those majority species showed little to no long-term hedging (i.e. browsing), as shown by form class (Table 5). For example, *Artemisia tridentata* was the most productive shrub in the area and produced 96% of the shrub-steppe shrub biomass, yet only one third of the 21 plants sampled showed moderate-high levels of hedging. High-elevation *Vaccinium scoparium* was the second most productive shrub recorded and was the dominant shrub in ABLA forest understories and parkland, yet showed moderate (46%) to high (17%) hedging. In riparian and meadow areas, 51% of the shrub biomass was produced by *Alnus incana*, which showed little to no browsing effects.

In the PSME cover types, *S. albus* and *Holodiscus discolor* were highly productive shrubs that were severely hedged (Table 4, Table 5). In ABGR stands, the dominant *Mahonia* spp. were

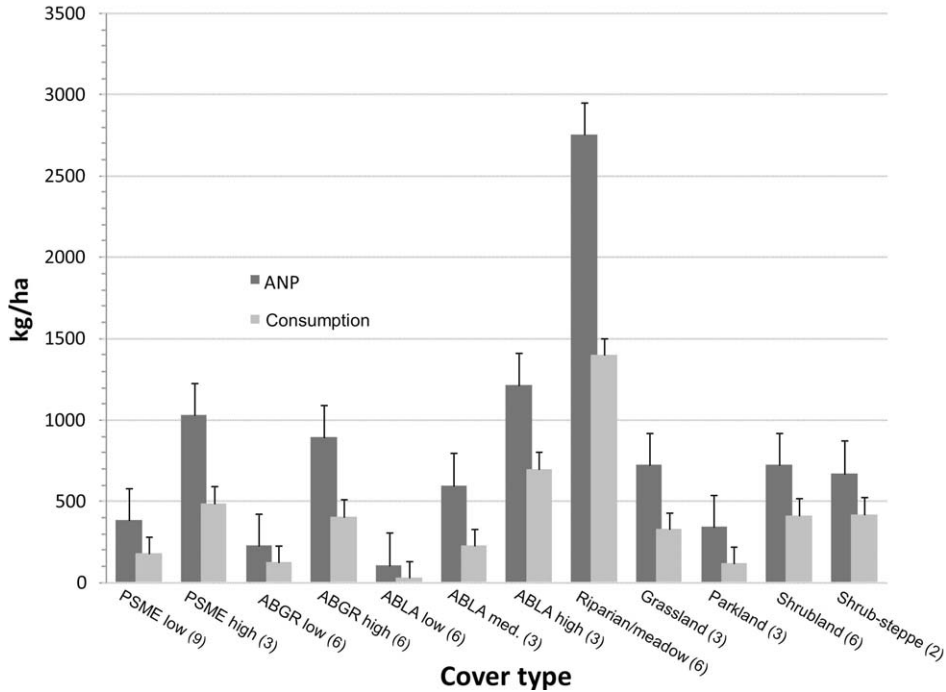


Figure 3. Mean and standard error of total above-ground net primary production (ANP) and utilization (all herbivores) in cover types in the Naches River basin in the southeastern Washington Cascade Range, 2005-2006. The numbers of sample locations follows cover type names in parentheses.

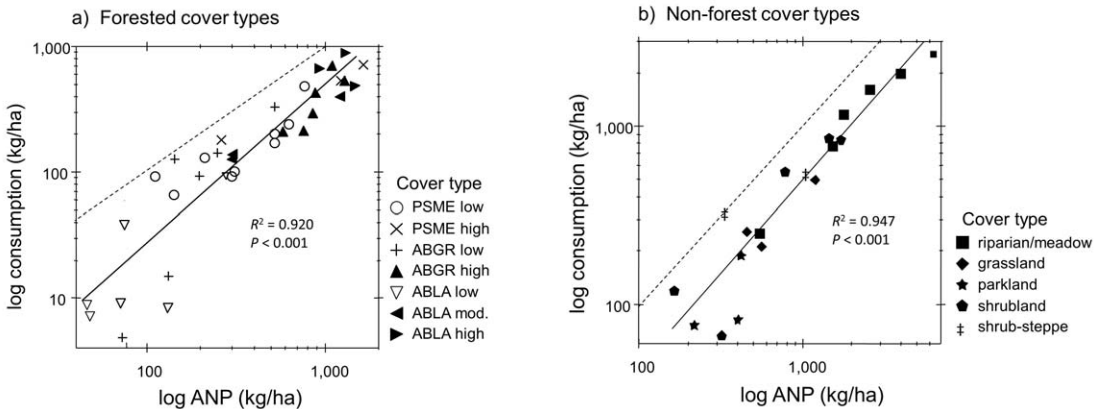


Figure 4. Utilization as a log-log linear function of above-ground net production in (a) forested and (b) non-forested cover types in the Naches River basin in the southeastern Washington Cascade Range, 2005-2006. Dotted line indicates utilization equal to production.

little browsed, but *Arctostaphylos nevadensis* showed moderate hedging. In ABLA cover types, *Ribes viscosissimum* was an abundant shrub with moderate (42%) to high (33%) hedging.

The most abundant and highly hedged shrubs in grassland, shrubland, and shrub-steppe cover types were *Artemisia arbuscula*, *A. rigida*, and *Purshia tridentata*.

TABLE 5. Proportion of shrub plants in growth form classes (BLM, 1996) sampled in the Naches River basin in the southeastern Washington Cascade Range, 2005-2006.

Species	Form class ¹								Count ²
	1	2	3	4	5	6	7	8	
<i>Abies amabilis</i>	0.96						0.04		23
<i>A. grandis</i>	0.69	0.29	0.02						42
<i>A. lasiocarpa</i>	0.93			0.07					15
<i>Acer glabrum douglasii</i> ³	0.29	0.43	0.29						7
<i>Alnus incana</i>	0.91		0.09						11
<i>Amelanchier alnifolia</i> ³	0.04	0.54	0.38	0.04					24
<i>Arctostaphylos nevadensis</i>	0.15	0.77	0.08						13
<i>Artemisia arbuscula</i>	0.14	0.29	0.57						7
<i>A. rigida</i>			0.50			0.50			8
<i>A. tridentata</i>	0.62	0.19	0.14	0.05					21
<i>Ceanothus velutinus</i> ³	0.20	0.20	0.60						5
<i>Chimaphila umbellata</i>	0.91	0.09							11
<i>Chrysothamnus viscidiflorus</i> ³	1.00								9
<i>Cornus sericea sericea</i>		1.00							1
<i>Ericameria bloomeri</i>	0.67	0.33							3
<i>E. nauseosa nauseosa</i>	1.00								2
<i>Eriogonum compositum</i> ³	1.00								1
<i>E. douglasii</i> ³	0.40	0.40				0.20			10
<i>E. heracleoides</i> ³	0.86			0.14					7
<i>E. microthecum</i> ³	0.90		0.10						10
<i>E. thymoides</i> ³	1.00								5
<i>E. umbellatum</i> ³	1.00								2
<i>Holodiscus discolor</i> ³		0.29	0.71						7
<i>Juniperus communis</i>	1.00								1
<i>Larix occidentalis</i>	1.00								1
<i>Ledum glandulosum</i>	1.00								3
<i>Linnaea borealis longiflora</i>	0.80	0.04		0.15					46
<i>Mahonia aquifolium</i> ³	0.72	0.24			0.04				25
<i>M. nervosa</i> ³	0.85	0.12		0.03					33
<i>Menziesia ferruginea</i>		1.00							5
<i>Paxistima myrsinites</i>	0.28	0.33	0.26	0.04	0.09				46
<i>Penstemon davidsonii</i>	0.75	0.25							4
<i>Philadelphus lewisii</i>		1.00							1
<i>Phlox diffusa</i>	0.88					0.13			8
<i>P. longifolia</i>	0.89			0.11					9
<i>P. speciosa</i>	1.00								2
<i>Picea engelmannii</i>	1.00								8
<i>Pinus albicaulis</i>	1.00								1
<i>P. contorta</i>	0.29	0.29	0.43						7
<i>P. monticola</i>	0.67	0.33							3
<i>P. ponderosa</i>	0.78		0.11	0.11					9
<i>Pseudotsuga menziesii</i>	0.64	0.28	0.08						25

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Species	Form class ¹								Count
	1	2	3	4	5	6	7	8	
<i>Purshia tridentata</i> ³		0.20	0.40			0.40			10
<i>Ribes lacustre</i> ³	0.20	0.40	0.30			0.10			10
<i>R. viscosissimum</i> ³	0.25	0.42	0.33						12
<i>R. watsonianum</i> ³		0.25	0.50	0.25					4
<i>Rosa gymnocarpa</i> ³	0.20	0.56	0.22	0.03					79
<i>Rubus leucodermis</i>		0.67			0.33				3
<i>Sambucus cerulea</i>		1.00							1
<i>Salix</i> spp. ³	0.63	0.38							8
<i>Salix scouleriana</i> ³		0.50	0.50						4
<i>Shepherdia canadensis</i>			1.00						1
<i>Spiraea betulifolia lucida</i> ³	0.34	0.50	0.13	0.02	0.02				56
<i>Symphoricarpos albus</i> ³	0.19	0.25	0.49	0.03	0.02	0.02			59
<i>Tsuga heterophylla</i>				1.00					1
<i>Vaccinium membranaceum</i>	0.10	0.50	0.35		0.02			0.02	48
<i>V. myrtillos</i>	0.67	0.17	0.17						6
<i>V. scoparium</i>	0.33	0.46	0.17	0.04					24
All species	0.46	0.30	0.18	0.03	0.01	0.02	0.00	0.00	807

¹ Form class: 1—All available (≤ 2.3 m above ground), little or no hedging.; 2—All available, moderately hedged; 3—All available, severely hedged.; 4—Partially available, little or no hedging; 5—Partially available, moderately hedged; 6—Partially available, severely hedged; 7—Unavailable; 8—Dead. Available forage was < 2.3 m above ground.

² The number of recorded shrub plants.

³ Elk key forage species in the study area.

Discussion

Several cautions about our data and results are appropriate. Sample sizes in cover types are not large, particularly for the shrub-steppe type, considering the extent and variability the landscape we tried to characterize; however, variability in production and utilization, in particular, is a common issue for range management (Holechek et al. 1995). We do not know the relative importance of specific herbivores (vertebrate or invertebrate) to apportion the observed utilization; but, we did not observe large numbers of invertebrate herbivores (e.g. grasshoppers), and among vertebrates elk likely were the main herbivore. We somewhat traded off a large spatial sample for repeated temporal replicates of the sample sites to estimate annual variation in habitat characteristics. We measured a suite of floristic and productivity variables to broadly characterize habitats vs. single-mindedly sampling production at more sample sites. We used two broad canopy-cover classes to characterize

the gradient of canopy cover found in nature; hence, our broad cover classes may simplify the variability of understory cover and production in relation to canopy cover. We have only 2 years of data: a “normal” temperature-moisture year and a somewhat dryer-than-normal year. Nevertheless, the data appeared to present a good first approximation of floristics, productivity, and utilization for the study area, as discussed below.

Forage Utilization

We found riparian and montane meadow cover types were the most important foraging habitats in our study area. Across all vegetation types, they were the most productive, supported the highest level of herbivory, and were the most species-rich cover types accounting for 29% of total production and an equal amount (29%) of the total herbaceous and shrub utilization, yet representing only 3% of the landscape. Our estimated ANP (2752 kg ha⁻¹) in this type was far

less than the 8440 kg ha⁻¹ of peak standing crop recorded in 2004 by Evans (2006) in 12-year old cattle+elk exclosures at 4 large meadows, some of which we sampled, in the Naches drainage of our study area. For those same exclosures, Beebe et al. (2002) reported a much lower average of 720 kg ha⁻¹ peak standing crop of graminoids and forbs during 1994 after 3 years of protection from cattle+elk grazing. Precipitation and temperature during the years Evans' (2004) and Beebe et al. (2002) studied these meadows was intermediate between our study years, so conditions during the growing season are unlikely to explain differences among studies in ANP estimates. Differences in experimental design (their exclosures vs. our caged plots) and field sampling (e.g., time of year, sample size, material collected, our pooling of riparian meadows and montane meadows) may account for differences in our ANP estimates and these studies. Our estimates from paired caged plots possibly overestimated ANP because we adjusted for negative utilization (i.e. more biomass outside cages than inside cages) in estimating ANP, a well-known and common sampling error for the caged-plot technique (Sala et al. 1988, McNaughton et al. 1996). However, not adjusting for negative utilization can yield nonsensical negative utilization rates (e.g., Stewart et al. 2006). Nevertheless, ANP in our riparian/meadow cover type was comparable to ANP for 8 mountain meadow sites in the Pacific Northwest reviewed by Milchunas and Lauenroth (1993).

Estimates of utilization were relatively similar among the 3 studies (Beebe et al. 2002, Evans 2006; this study) of meadows in our study area, regardless of reported differences in ANP among studies. We estimated 57% utilization of herbaceous (non-shrub) ANP by cattle and elk with our paired caged-plot technique. Combined utilization by livestock and elk was 67% in Evans' study and 66% in Beebe et al., as estimated by the ratio of standing biomass in the exclosure open to cattle and elk grazing compared to standing biomass in the full exclosure (i.e. no grazing). Comparing our cage-plot data and their exclosures assumes that grazing did not depress or facilitate production in our caged plots (Bartolome 1993, Painter and Belsky 1993).

The 3-way exclosures used by Evans (2006) and Beebe et al. (2002) allowed them to exclude cattle to estimate elk and deer utilization at 50% (Evans) and 43% (Beebe et al.), respectively; thus, 65-75% of the total utilization in their meadows was by elk and deer. A 65-75% share of total meadow utilization by elk and deer is 25-35% less than an expected 90% based on their proportion of the total AUM stocking rate estimated for the study area. Conversely, livestock consumed 25-35% of the total meadow utilization, a share larger than expected from their 10% share of the total stocking rate. A relatively higher rate of utilization by cattle than elk in meadows is to be expected based on the well-known grazing preferences of cattle for grass forage on gentle topography (Skovlin et al. 1976, Wisdom and Thomas 1996, Holechek et al. 1995,) and the general avoidance of cattle by elk (Wisdom and Thomas 1996, Coe et al. 2001, Stewart et al. 2002).

Other studies in the western U.S. have reported utilization by wild ungulates in non-forest cover types similar to the 43-50% range reported by Beebe et al. (2002) and Evans (2006): 35% in dry meadow communities in the nearby Blue Mountains of Oregon (Stewart et al. 2006); 45% in a wide elevational range of grasslands and meadows in Yellowstone (Frank and McNaughton 1993); and, 55% in low elevation grasslands in Yellowstone (Singer and Harter 1996). Our reported rate of 57% total utilization (livestock and wild ungulates) slightly exceeds the acceptable standard of 40-50% "moderate" utilization for the Wenatchee National Forest (WNF 1990), and fits a general 50% standard for moderate utilization of montane grasslands in the Pacific Northwest (Hedrick 1958, Guinn 1994). Skovlin et al. (1976), however, recommended utilization rates of 30-40% for mixed forest and grassland ecosystems of the interior Pacific Northwest, although that recommendation pertains mainly to livestock grazing.

The relatively small contribution of shrubs to total ANP and the forage base (mostly < 10%), as well as relatively overall low (4%) utilization, likely belies their seasonal importance in livestock and elk diets. Shrubs can be an important component of diet quantity and quality, especially during the late summer and fall when livestock and elk

foraging shifts from open-forest stands to more closed-canopy stands (Korfhage et al. 1980, Cook 2002, Long et al. 2008a, Long et al. 2008b). We documented high long-term grazing impacts on some species of typical and atypical forage shrubs (Cook 2002), such as *Symphoricarpos albus*, *Holodiscus discolor*, and *Arctostaphylos nevadensis* in mid-elevation PSME and ABGR cover types, *Ribes viscosissimum* in high-elevation ABLA cover types, and *Artemisia arbuscula*, *A. rigida*, and *Purshia tridentata* in low-elevation non-forest cover types.

Impacts on shrubs are likely underestimated because historically high levels of herbivory by wild ungulates and livestock in the study area (Mitchell and Lauckhart, 1948; Wissmar et al., 1994) may have suppressed or eliminated highly-palatable shrubs (Tiedemann and Berndt 1972, Riggs et al 2000, Alldredge et al. 2001, Kie and Lehmkühl 2001, Manier and Hobbs 2007). In similar PSME and ABGR forests in the nearby Blue Mountains of southeastern Washington and northeastern Oregon, Riggs et al. (2000) found ungulate herbivory seriously depressed biomass of shrub genera *Acer*, *Linnaea*, *Amelanchier*, *Salix*, *Sorbus*, *Ceanothus*, *Physocarpus*, and *Rubus* outside of 25-year-old exclosures, where understory biomass was 2x greater than outside exclosures. Johnson (2007) found the shrubs *Rosa*, *Symphoricarpos*, and *Purshia* increased dramatically in the absence of long-term browsing in shrubland communities in the Blue Mountains. Tiedemann and Berndt (1972) reported 5 times more shrub cover, primarily *Ceanothus velutinus* with *Amelanchier alnifolia*, *Prunus virginianus*, and *Symphoricarpos albus*, inside vs. outside a 30-yr-old exclosure in a *Pseudotsuga menziesii*/*Calamagrostis rubescens* habitat type dominated by ponderosa pine with Douglas-fir.

Across all the other cover types we measured, annual utilization rates as a proportion of ANP were relatively similar across the range of cover type productivity, except for lesser utilization in some low-productivity ABLA, ABGR, and PSME sites. If animals optimize their intake by foraging in the most productive cover types (Senft et al. 1987, Bailey et al. 1996, Anderson et al. 2008), then we might have expected utilization rates to increase with site productivity above some threshold of low

production. The observed relatively even pattern of utilization across a range of ANP in the landscape might be a function of processes operating at the scales of annual home range, feeding site (i.e., a collection of patches), and patch (Bailey et al. 1996). Utilization within a particular cover type is constrained by seasonal availability (e.g. snow) and the production and maturation of forage along the elevational gradient, so that ungulates move in response to increasing forage quantity and quality (Skovlin et al. 2002).

Under the Forage Maturation Hypothesis, animals select cover types at intermediate stages of production to maximize the trade-off between forage quantity and quality (Fryxell 1991, Wilmshurst et al. 1995, Hebblewhite et al. 2008). That tradeoff can occur along the elevational gradient of cover types (Hebblewhite et al. 2008), but also at the scale of feeding sites during the non-winter season. During spring and early summer, elk forage in open forest and non-forest cover types where early phenology provides a relatively high quantity and quality of forage, then during mid- and late-summer elk switch to foraging in forested cover types where phenology is delayed and quality remains high (Skovlin et al. 1989, Long et al. 2008a, Long et al. 2008b). Relatively high rates of utilization in low-productivity cover types could result from feeding in suboptimal cover types to maximize forage intake while traveling (Senft et al. 1987), from regular sampling of forage in all patches in feeding sites or seasonal home ranges (Westoby 1974, Bailey et al. 1996), or from selection of habitats for other reasons (e.g., vulnerability to hunters, calf security) (Skovlin et al. 2002). Foraging and sampling while traveling are highly plausible if elk residency at high-value sites is a function of multiple visits vs. slowing movement at favorable locations (Ager et al. 2003, Kie et al. 2005, Forester et al. 2007, Anderson et al. 2008).

Moderate levels of utilization (~50%) across all cover types have important implications for resource selection analysis that uses simple standing-crop biomass estimates (e.g., Merrill 1994, Beck and Peek 2004, Anderson et al. 2005). The timing of measurement of standing crop will be critical for gaining unbiased estimates of what ungulates may encounter and how that affects

resource selection and animal fitness. Typical measurement of peak biomass at the end of the summer growing season will underestimate the value of cover types with an early phenology and utilization period by a factor comparable to the utilization rate.

Exotic Species

Despite estimated moderate utilization, riparian/meadow cover types supported the highest cover (18.5%) and richness (13%) of exotic species among cover types. The exotic grass *Poa pratensis* had the highest cover among all riparian/meadow species and was an indicator species in our riparian/meadow cover types along with the exotic forb species *Plantago lanceolata* and *Trifolium repens*. *Poa pratensis* is known to be a highly invasive and grazing-resistant rhizomatous grass in meadows (Mack and Thompson 1982, Frank and McNaughton 1993, Singer 1995) that persists long after grazing ceases (Daubenmire 1988, Singer 1995, Stohlgren et al. 1999). After three years of protection in the Naches three-way exclosures (cattle+elk, elk-only, no grazing), Evans (2006) and Beebe et al. (2002) found that *Poa pratensis* remained the dominant meadow species with importance values three times higher than the second-ranked species. Evans reported percent cover of exotic species (4-26%) in three of four meadows with elk and cattle+elk grazing that was roughly comparable to our estimate, but 65% cover of exotic species (mostly *Cichorium intybus*, *Plantago lanceolata*, *Poa pratensis*, *Bromus hordeaceus*) in a fourth meadow.

The presence of these exotic species in grazing lands is a legacy of heavy historical grazing by domestic and wild ungulates (Wissmar et al. 1994, Mitchell and Lauckhart 1948) that can be sustained by moderate wild ungulate grazing (Frank and McNaughton 1993, Singer 1995, Rexroad et al. 2007), and by recent managed livestock grazing. That also seems to be the case in our meadows and for dry grasslands and shrub-steppe where exotic *Bromus tectorum* was an important species that has persisted long after the cessation of heavy grazing on dry sites (Mack and Thompson 1982, Daubenmire 1988). Evans (2006) found little significant

difference in exotic cover between Naches-area meadows grazed by cattle+elk and elk-only. One might hypothesize that complete protection from grazing could result in restoration of dominance by native species and the reduction of exotic and other species richness in relatively productive mesic, but not dry, cover types (Olf and Ritchie 1998, Proulx and Mazumder 1998, Osem et al. 2002, Bakker et al. 2006). For example, Johnson (2007) reported *P. pratensis* declined in meadows protected from grazing for about 50 years in the Blue Mountains of Oregon. However, both complete short-term (3-year) (Beebe et al. 2002) and longer-term (12 years) (Evans 2006) exclusion of grazing in 4 large Naches meadows showed the predicted response in only 1 meadow where exotic species dominated the site (65% of the plant cover). Evans found the response varied in the other 3 meadows where native species dominated plant cover: exotic cover increased and exceeded native cover; both exotic and native species cover increased equally; and, exotic cover increased 5x compared to grazed conditions while native cover did not change. Thus, exotic species can persist long after the primary grazing impacts (Keeley et al. 2003), and response to protection from grazing can be highly idiosyncratic depending on local species composition, environmental conditions, and scale of measurement (Stohlgren et al. 1999, Collins et al. 2002).

Forest Restoration

Proposed forest restoration management (mainly our PSME and dry ABGR types) to reduce uncharacteristic fuel loads and restore resilient stand structures and processes (Agee and Skinner 2005, Noss et al. 2006, Collins et al. 2010) likely will increase the forage base for ungulates by opening the canopy to <40%, as shown by our data, and stimulating understory development (Hedrick et al. 1968, Skovlin et al. 1989, Lyon and Christensen 2002, Vavra et al. 2005, Long et al. 2008b; but, see Sutherland and Nelson 2010). Opening the canopy of long-closed stands with diminished seed banks of herbaceous species might increase invasive species cover (McGlone et al. 2009, Sabo et al. 2009; but see Wienk et al. 2004); however, responses of invasive species can vary consider-

ably due to site conditions (Sutherland and Nelson 2010) and can be mitigated by management (e.g., weed control along roads). Locally in dry forests of eastern Washington State, Nelson et al. (2008) reported only a small (2%) increase in cover of exotic species in a large retrospective sample of thinned and burned stands.

The spatial arrangement of treatments across the landscape might strive to replicate the patchy mosaic of stand structure created by environmental and disturbance-caused heterogeneity (Agee 2003, Brown et al. 2004, Hessburg et al. 2005) and to maximize the seasonal abundance of forage in open- and closed-canopy forests (Skovlin et al. 1989, Skovlin et al. 2002, Long et al. 2008a, Long et al. 2008b). An implication of our finding that most forest and non-forest cover types are utilized is that treatment in any type likely will increase the utilized forage base, depending on the inherent productivity of the site (Vavra et al. 2005). The best options for increasing production appear to be closed-canopy conditions on aspects that had the highest production: ABLA stands on south-aspects, PSME stands on north-aspects, and ABGR stands on all aspects. ABGR stands, in particular could be expected to produce abundant shrub forage because high-productivity in ABGR stands was primarily a function of open canopy alone, not the interaction of canopy cover and aspect as with PSME and ABLA types (Table 1).

Dry forest restoration could be spatially allocated in several ways to either increase the forage base or reduce utilization in some locations (Wisdom and Thomas 1996, Gordon et al. 2004), contingent on maintaining elk populations at the same level relative to carrying capacity (Kie et al. 2003) and providing adequate security cover (Lyon and Christensen 2002). One objective may be to reduce utilization of particular locations where high site fidelity may result in persistent use (e.g. Kaufmann et al. 2010), primarily, meadows with high exotic cover that are targeted for restoration. Forest restoration treatments might be placed in the vicinity of target sites to increase the surrounding forage base, because elk residency in a particular location is a function of many separate visits to the site, the frequency of which is a function of both

the location's forage availability and the ability of the surrounding area to support other activities (e.g. resting) (Forester et al. 2007, Anderson et al. 2008). Another option is to target suspected travel routes where elk are most likely to encounter and use restored sites. Kie et al. (2005) found strong directionality of elk movements parallel to ridgelines along hill slopes and along lower slopes adjacent to highly productive and utilized riparian areas. A final consideration is the temporal spacing of treatments across the landscape due to the relatively short-term (~5 years) spike in nutritional value of forage in thinned and burned areas (Skovlin et al. 1989, Long et al. 2008b).

This paper presented a broad survey of forage dynamics across a large and heterogeneous landscape, and discussed implications for ungulate resource selection analyses and forest restoration. Additional research might focus on intensive sampling of composition, production, and utilization of the most productive forest cover types, and winter range, to better document that variability and provide more exacting estimates of production for estimation of carrying capacity. Establishment of a network of forest and range exclosures would allow exacting quantification of the impacts of herbivory on herbaceous and shrub species. Exclosures would provide forest and wildlife managers with data on the potential impacts of changing patterns of herbivory from altered numbers or distribution ungulates stemming from management or by a likely recolonization by wolves (*Canis lupus*) from a breeding pack 15 km northeast of the study area (WDFW 2012). Our results and the discussion of potential effects of forest restoration treatments serve as hypotheses for testing in studies of stand- and landscape-scale treatment effects and ungulate resource selection and productivity.

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